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CHEMICAL AND VIBRATORY COMMUNICATION IN THE AQUATIC PISAURID SPIDER *DOLOMEDES TRITON*

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ABSTRACT

Male *Dolomedes triton* perform announcement displays consisting of leg-waving and jerks in response to water that has contacted the integument of female conspecifics. Jerks cause bursts of concentric surface waves that probably provide a signal for the female. Males also follow the female's dragline, using a lycosid-like manner on land but switching to rowing and pulling when the line is on water. When close enough to touch the female, the male performs a courtship display consisting of rapid leg tapping, which, with the female's leg-waving, results in prolonged leg interplay between the sexes.

INTRODUCTION

The role of chemical communication in various families of spiders was reviewed recently by Tietjen and Rovner (1982). Its use by pisaurid spiders was established experimentally by Kaston (1936), following earlier suggestions by Bonnet (1924) and Bristowe and Locket (1926). Carico (1973) included some comments on the probable role of chemoreception during reproduction in *Dolomedes*, while Williams (1979) examined its importance for predation in this genus.

Our present investigation centered largely on three questions about chemical communication in *Dolomedes triton* (Walckenaer): (1) Does its pheromone persist on wet surfaces and water? This is not the case in those species of the closely related lycosid spiders so far studied, in which water inactivates the substance (Dondale and Hegdekar 1973, Tietjen 1977). (2) Do male pisaurid spiders follow female draglines? Dragline-following in T-mazes has been studied in lycosids (Dijkstra 1976) and in agelenids (Krafft and Roland 1979, Roland in ms.). Following of draglines in open arenas has been examined in various lycosids (Engelhardt 1964, Richter 1972, Tietjen 1977, Tietjen and Rovner 1980). (3) Can male spiders follow female draglines on water? Our observations and experiments indicate the answer to all three questions to be "yes." In addition, we provide descriptive data on other aspects of pre-copulatory behavior in *D. triton*, including the likelihood of communication by surface waves in such aquatic spiders, previously suggested by Bristowe (1958).

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GENERAL METHODS

Penultimate and adult *D. triton* were collected along the margin of Dow Lake in Athens County, Ohio, during June and July, 1981. Spiders were housed individually in plastic cages (13 X 7 X 7 cm high), each cage having a paper floor and a cotton-stoppered vial of distilled water. Mealworm larvae *(Tenebrio)* or cockroaches *(Periplaneta)* were offered two or three times weekly. Room temperature usually was 25° (range, 23°-27°). Lighting in the windowless room remained on a 12-hr light/12-hr dark cycle. We filmed behavior with a Bolex Super-8 Macrozoom 160 camera at 18 frames/sec and a Cine-8 high-speed camera (Visual Instrumentation Corp., Model SP-1) at 100 frames/sec.

Individuals providing stimuli in Experiments 1, 2, 3, and 5 were housed in glass-topped 5-gal aquaria (41 X 21 X 26 cm high), which were filled with water to a depth of 5 cm. (Since tap water was used, freshly filled aquaria stood for one day before introduction of the next resident.) A strip of wood (20 X 3.5 X 0.6 cm) placed on the water at one end of the aquarium served as a resting site for the spider, which typically remained with two or three anterior leg tarsi floating on the water. Residents were housed in their aquaria for at least two days prior to the use of these aquaria in experiments. Aquaria used to house males had never been used previously for females. (Separate brushes and jars for each sex were used when transferring spiders from one container to another.) In these experiments the aquarium resident was removed and the male introduced to the half of the water surface opposite that containing the resting site. Thus, males were never placed initially at the location where the resident spent most of its time and never were placed in an aquarium that simultaneously contained another spider during these tests for responsiveness to potential chemical stimuli.

DESCRIPTION OF PRE-COPULATORY BEHAVIORS

Announcement Display.—After introduction to the aquarium of an adult female or after contacting her dragline on land or water, the male begins the first phase of signaling. This involves "leg-waving" and "jerks." The former includes lifting legs I, usually in irregular alternation, but sometimes synchronously, with these legs typically being held extended straight or just slightly arched (Fig. 1). Most often, the tarsus describes a vertically elliptical path. On land the male walks with slow, erratic movements

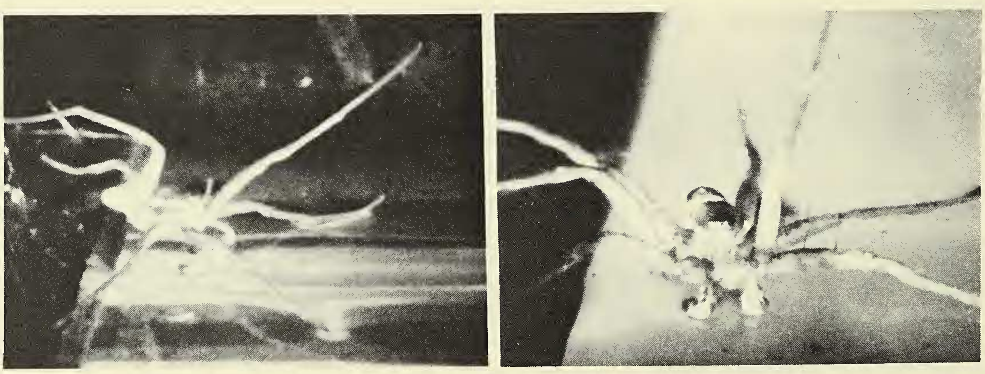

Fig. 1.—Lateral and front views of a male *Dolomedes triton* performing leg-waving (leg I stiffly elevated) while entering the water from the female's resting site and while moving on the water, respectively. (Photographs of frames of Super 8 mm movie film exposed at 18 frames/sec.)

and places his own dragline as he advances. On water his body is close to the surface, his legs almost horizontally extended, and his palps rest on the surface in a tightly flexed position. When the presumed chemical stimulus is strong, the very high lifting of legs I gives way to rapid, simultaneous tapping movements, especially on land.

At irregular intervals, while holding all the legs in contact with the substrate, the male performs one to three "jerks." Each results from one or, more typically, two partial flexions and extensions at the femoro-patellar joint of legs I and, to a much less degree, legs II. A noticeable effect of the jerk on water is a single or double burst of concentric surface waves spreading outward from the male. Each burst results from a downward thrust of the anterior legs as they jerk in the above-described movement. When the spider is on land, the jerk is a much less obvious behavior due to the absence of the easily seen surface waves that attract our attention when the spider is on water.

Courtship Behavior.–As mentioned above, behaviors that presumably provide two long-distance signals–leg-waving (probably visual) and jerks (probably vibratory)–give way to close-range signaling when the female pheromone is in high concentration. This occurs when the male contacts the resting site, the female herself, or, in some cases, the silk draglines of the female. He then begins to perform rapid simultaneous tapping of legs I, both legs being lifted a relatively short distance above the substrate, with quivering of the distal segments. The male continues to lay down his own dragline.

In response to the male's approach, the female may briefly "drum" on the substrate, including the water surface, by rapidly vibrating her palps; on water, surface waves result from this behavior. She then performs a behavior that is like a slow and exaggerated version of the male's earlier leg-waving. Her legs I and/or II are waved in broad, circular paths while held rather stiffly extended. Leg interplay results from the male's leg-tapping and the female's leg-waving, such an interaction having been noted in *D. scriptus* for one-half hour prior to copulation (Carico 1973).

RESPONSES OF MALES TO VARIOUS WATERS

1. Aquarium of Male.–Method: We used 15 males in a series of 20 tests for responsiveness to aquaria that had housed five other males. In 10 trials, test males had been housed in aquaria of their own; in the other 10, test males had been housed in plastic cages with paper floors.

Results: None of the males showed jerks, leg-waving, or agonistic display within 10 min after introduction to the water surface.

2. Aquarium of Intact Female.–Method: Ten males were used in 20 tests for responsiveness to aquaria that had housed nine intact females.

Results: Leg-waving and jerks occurred within the 10-min test time in 16 of the 20 tests. In 14 of the 16 cases this behavior began on the water surface, prior to contact with the female's wooden resting site.

3. Aquarium of Female with Sealed Spinnerets.–Method: We used 11 males in 20 tests for responsiveness to aquaria that had housed one of three females whose spinnerets had been sealed with paraffin at least two days prior to testing.

Results: Leg-waving and jerks occurred within the 10-min test time in 10 of the 20 tests.

4. Water Contacting Silkless Female for One Hour.–Method: We wished to determine if males would respond to water that had contacted the female's integument for a relatively short time, as well as to minimize the possibility that responses in aquaria resulted from an airborne component that accumulated above the water surface. We used five females with sealed spinnerets in a total of 20 tests. For each test, a female was placed into a covered plastic vial containing 50 cc of distilled water. The vial was turned over at 5-min intervals to insure adequate contact of the female with the water. After 1 hr the female was removed and the water poured into a shallow bowl (19 cm in diameter). The test male (nine were used) was placed on the water surface and observed for 10 min.

Results: Leg-waving and jerks occurred in five of the 20 tests.

5. Aquarium of Intact Female Restricted by Screening.—Method: We wished to prevent the female from wandering more than about 10 cm beyond her wooden resting site, so that, unlike Exper. 2, the male could not directly encounter water through which the female might have swum, or on which she might have walked. We mounted a piece of plastic window screening obliquely from the top to the bottom of each of two aquaria (Fig. 2). Any pheromone produced by the female would have to disperse from the release area near the resting site. The flaw in this design arose from the tendency of females to hang from the screen—well above the water—rather than use the resting site. We urged them down to the water-level resting site each day, so that at least part of each day included contact with the water.

We used 10 males in a total of 20 tests for responsiveness to the aquaria of 3 intact females. For each test the female was removed and a glass barrier placed in the middle of the aquarium. Thus, during the initial phase the male could neither touch any surface that the female had directly touched (the screen included) nor any of her draglines. After spending 10 min on the water beyond the glass barrier ("A" of Fig. 2), he was transferred to the female's living area ("B"). If he did not court in the latter area within 10 min, we assumed him to be sexually unresponsive and did not include his behavior in the 20 tests. Thus, all the males included in the scoring for this experiment were ones that at the least responded to the presumably adequate concentration of pheromone in area B.

Results: Leg-waving and jerks were shown by males in area A in five of the 20 tests. (Results of Experiments 1-5 are summarized in Table 1.)

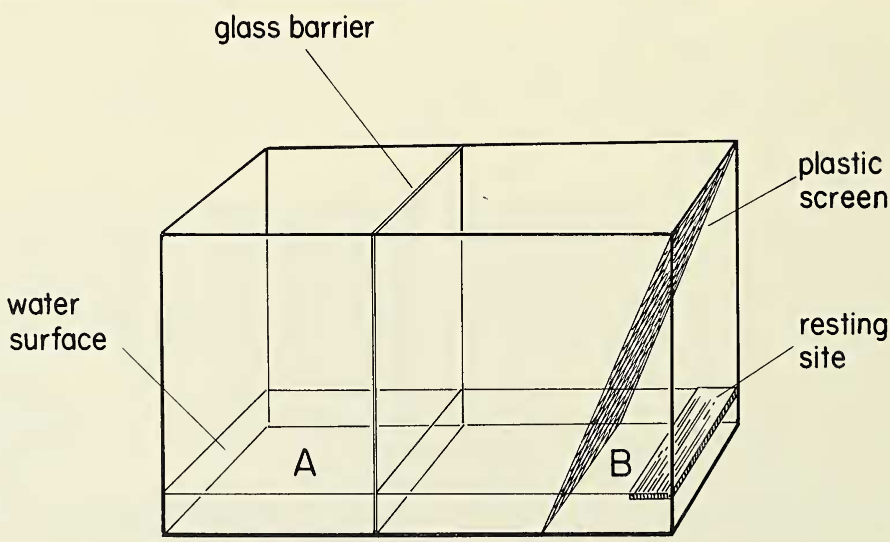

Fig. 2.—Setup for Experiment 5. A female *Dolomedes triton* is restricted to area B of the aquarium for several days by a plastic screen. She is removed, a glass barrier is inserted, and a male is introduced to the water surface in area A. After 10 minutes he is transferred to area B.

RESPONSES OF MALES TO VARIOUS DRAGLINES

a. **Conspecific Adult Female Dragline (Dry Substrate).**–Method: We combined two methods developed by previous workers to obtain single draglines from spiders. The substrates were those used by Tietjen (1977): glass plates (41 X 5 cm) to which three glass rods had been glued transversely at 10-cm intervals. This insured that most of the line would be elevated about 0.5 cm (the rods' diameter) above the plate, enabling males to follow while walking. We used Work's (1981) method to force the spider to place the line lengthwise along the plate (and over the rods). The spider was put beneath an inverted beaker at the " start" area at one end of the plate. After the spider fixed an attachment disk to that site, we guided it slowly along the plate beneath the slightly raised beaker. At the other end of the plate, about 30 cm away, we waited until a second disk was attached, urged the spider off the plate, and used masking tape to secure this next short section of dragline to the plate. Seven males were used to test the lines of four females in a total of 10 tests.

Results: After introduction to the start area, the male typically encountered the female's dragline during chemoexploration of the glass surface, the palps brushing against the substrate, as is well-known in lycosids and other wanderers. Leg-waving, leg-tapping, or jerks sometimes began even before the dragline itself was contacted, suggesting that pheromone was deposited on the glass during the female's brief rest at that site. After encountering the line, the male straddled it and advanced along its length, using his palpal tarsi (medial surface) and legs I to touch the line. Palpal stroking of the line thus was like that described for *Lycosa* spp. by Tietjen and Rovner (1980). Tapping or grasping the line with the claws of either leg I occurred at variable intervals. Following occurred in nine of the 10 tests.

b. **Conspecific Male Dragline (Dry Substrate).**–Method: Thirteen males were used to test the lines of seven adult male conspecifics in a total of 20 tests.

Results: In six of 20 tests, the dragline was followed a short distance (< 1/3 of the line); however, neither leg-waving nor jerks occurred.

c. **Conspecific Subadult Female Dragline (Dry Substrate).**–Method: Fourteen males were used to test the lines of two subadult female conspecifics in 20 tests.

Table 1.–Summary of experiments on *Dolomedes triton.* (Except for d, all experiments involve conspecifics; unless stated otherwise, all involve adults).

Stimulus situation	Tests yielding display	Total no. of tests	Tests yielding following	Length of line followed
1. Aquarium of male	0	20	–	–
2. Aquarium of female	16	20	–	–
3. Aquarium of silkless female	10	20	–	–
4. Water contacting silkless female	5	20	–	–
5. Aquarium of restricted female	5	20	–	–
a. Dragline of female	9	10	9	entire
b. Dragline of male	0	20	6	< 1/3
c. Dragline of subadult female	0	20	6	< 1/3
d. Dragline of heterospecific female	0	20	5	< 1/3
e. Dragline of female on water	9	10	9	entire

Results: As in (b), six cases of partial following without sexual responses occurred in the 20 tests.

d. Heterospecific Adult Female Dragline (Dry Substrate).—Method: Eleven males were used to test the lines of four adult female *Lycosa rabida* in 20 tests.

Results: Five cases of partial following without sexual responses occurred in the 20 tests.

e. Conspecific Adult Female Dragline On or Just Below Water Surface.—Method: After obtaining the draglines, we put the glass plates into empty 10-gal aquaria. Then we poured distilled water slowly onto the aquarium floor until the level reached the top of the glass rods, i.e., until the water surface was just below, equal to, or slightly above the dragline, depending on the section of the line. One of five males then was introduced to the water in the start area.

Results: Following of the entire line, accompanied by leg-waving and jerks, occurred in nine of the 10 tests. In following, the male rowed along, with legs II and III providing the propulsion. The palpal tarsi rested on the water, strongly flexed, and were not used to stroke the line. The fourth legs dragged behind, while legs I were used to locate and pull on the line: After swinging broadly across the surface, the right or left leg I eventually located the line and grasped it with the claws. The spider then used this leg to pull forward, this being the second method of advancing along the line (Fig. 3). (Results of Experiments a-e are summarized in Table I.)

DISCUSSION

Kaston (1936) had demonstrated the existence of a courtship-eliciting, ether-soluble substance on the integument of female *Dolomedes scriptus*. He also showed that a sex pheromone was bound to the female's silk but was not released onto the substrate simply by contact of the integument with the cage floor. Our primary purpose was to examine the nature of such chemical signaling on a watery substrate, a more natural situation for such aquatic species as *D. scriptus* and *D. triton*. We also wished to find out if male pisaurid spiders follow draglines and if courtship in another member of the genus *Dolomedes* resembled that described by Kaston (1936) for *D. scriptus*.

In response to the presence of a presumed female sex pheromone, male *D. triton* show leg-waving and jerks, the latter being a distinctive indicator of sexual excitement in males on water due to the production of concentric surface waves. When the pheromone concentration is high, especially on contact with the female or her resting site, the announcement display of leg-waving and jerks gives way to rapid leg-tapping. If the female waves her legs I and II in response, prolonged bouts of leg interplay between the partners result. Thus, pre-copulatory behavior is triggered chemically and then includes vibratory and tactile signals. Leg-waving may also yield visual signals. While pre-copulatory behavior shares some elements with that of *D. scriptus* (Kaston 1936), *D. triton*'s jerk is an important addition. We anticipate that future experiments will reveal a communicatory function for the surface waves produced by the male's jerk (and perhaps for the female's palpal "drumming", which also produces concentric surface waves). The resemblance to the surface wave signals of water striders (Hemiptera, Gerridae), well-studied by Wilcox (1972, 1979), is suggestive of such a function.

Contact with the water of a female's aquarium usually triggers pre-copulatory behavior in males (Exper. 2), whereas a male's aquarium does not (Exper. 1). Silk from the female need not be present on or in the water to yield a medium level of responsiveness in males (Exper. 3); however, the level of positive responses is higher when the female has been in contact with the water for days rather than only for 1 hr (Exper. 4). The occurrence of some responses to the water poured into the bowl from the vial (Exper.4) indicates that the responsiveness of males in the previous experiments did not depend on an airborne component that built up over the water in the aquarium, although such a factor could contribute to the total effect. One would not expect olfaction to be important in *D. triton* on the basis of Kaston's (1936) having found no role for it in *D. scriptus.*

Based on the above experiments, as well as Exper. 5, we hypothesize that the pheromone secreted onto the female's integument also spreads out on the surface of the water, as would a non- or mildly polar compound– perhaps a lipid or steroid. Sarinana et al. (1971) had postulated that the sex pheromone on the lycosid spider *Pardosa ramulosa* was a lipid, based on solubility characteristics, supporting the earlier view of Kaston (1936) on this subject.

Since female *D. triton* remain at the same site for days and remain motionless at one spot on the water for up to at least 2 hr (J. Sefton and Rovner, unpubl.), it seems possible to have a build-up of pheromone on the water surrounding the female. Thus, male *D. triton* could detect the female before touching her dragline or making visual or direct contact with her. The male's signals in response, likewise effective day or night, probably inhibit the female's predatory behavior. Indeed, several instances of cannibalism did occur when males failed to respond to the water of aquaria containing what we assumed were food-sated females during later pairings undertaken to study male-female interactions.

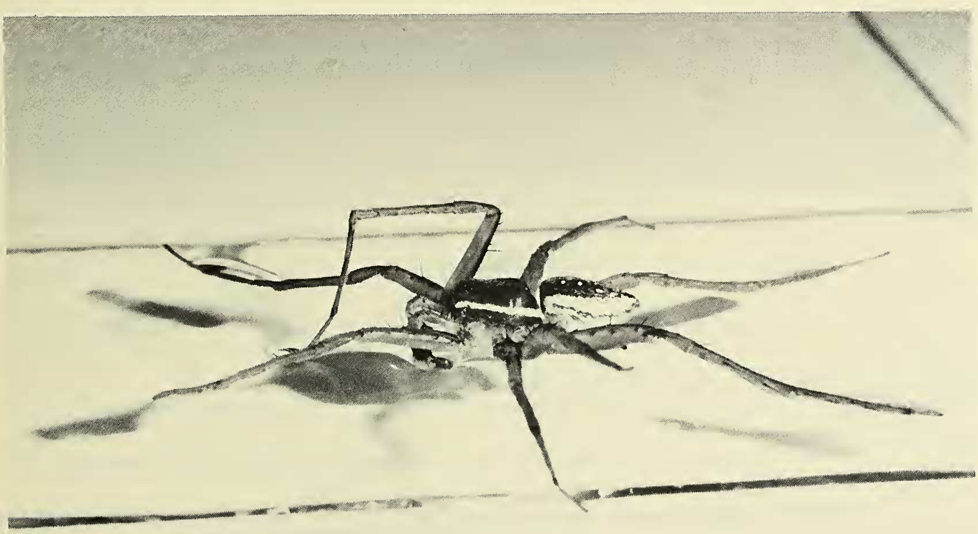

Fig. 3.–Dragline-following on water by a male *Dolomedes triton.* The spider is advancing along the silk thread (not visible) by grasping it with the claws of one foreleg and pulling himself forward; the arched right foreleg has just completed such a pull. Rowing movements of legs II and III also aid forward progression.

Male *D. triton* may partially follow the draglines of conspecific males (Exper. b) and subadult females (Exper. c), as well as heterospecific females (Exper. d); however, they do not show sexual responses. The tendency to respond to silk, irrespective of a chemical that may be present or absent on it, has most recently been seen in studies using T-mazes that involved agelenids (Roland in ms.). Apparently, lacking the adequate chemical stimulus of the female pheromone, the "incorrect" threads still provide sufficient mechanical and possibly some general chemical stimuli to elicit low levels of following behavior in some males. The distinction between chemical and mechanical cues in dragline-following by lycosids was well-demonstrated by Tietjen (1977), who found that imitation lines—even human hairs—would be followed for some distance by males that were already in a following mode from chemical stimulation.

On both dry substrates (Exper. a) and water (Exper. e), male *D. triton* readily follow adult female's draglines. Thus, the pheromone bound to the silk of these aquatic spiders must be unlike those used by various lycosids, which are degraded by water (Dondale and Hegdekar 1973, Hegdekar and Dondale 1969, Tietjen 1977). Instead it may turn out to be a mildly polar compound, as has been suggested for the silk-bound female pheromone of the salticid *Phidippus audax* (N. Oden, pers. comm.) or a non-polar compound. Of course, whether the dragline of *D. triton* retains its potency on water as long as it does on land remains to be determined. Nevertheless, the ability of males to advance along the line by rowing and pulling enables them to locate the female when the male is approaching via the water surface. Thus, a long-distance, orientational role for chemical signaling on water can be added to the close-range, courtship-eliciting aspects that were examined in Kaston's (1936) pioneering work on *D. scriptus* and other wandering spiders.

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